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PREDATION AND VARIATION IN BREEDING HABITAT USE IN THE OVENBIRD, WITH SPECIAL REFERENCE TO BREEDING HABITAT SELECTION IN NORTHWESTERN PENNSYLVANIA

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ABSTRACT.—From 1971 through 2003, Ovenbirds (*Seiurus aurocapilla*) at the Hemlock Hill Biological Research Area in northwestern Pennsylvania never bred in forest interior. Instead, they exhibited atypical habitat selection for breeding by occupying regenerating forest edges. Pairs in 14 territories, the entire population, showed normal annual return rates and pairing rates compared with other studies. For this ground-foraging bird, other studies showed that deep soil litter is preferred—but at my study site, soil litter depth in Ovenbird-occupied areas was lower than that found in the unoccupied forest interior. During May, July, and August, songs played in forest interior to attract Ovenbirds to settle there were unsuccessful. I tested the hypothesis that eastern chipmunk (*Tamias striatus*) abundance influenced this atypical habitat selection. Chipmunks were nearly absent from Ovenbird territories, but were abundant in the forest interior. I discuss habitat selection in birds in relation to simple cues and relate this to variation in habitat selection and use found in Ovenbirds. *Received 29 December 2004, accepted 9 August 2005.*

The Ovenbird (*Seiurus aurocapilla*) is a classic example of a “forest interior” and “area sensitive” songbird (Frost 1916, Forman et al. 1976, Ambuel and Temple 1983, Kroodsmma 1984, Gibbs and Faaborg 1990, Freemark and Collins 1992). In some areas, it avoids edge habitat altogether, irrespective of forest patch size (e.g., Missouri; Van Horn et al. 1995), but in other areas it does not appear to do so (e.g., New Brunswick [Sabine et al. 1996], Saskatchewan [Mazerolle and Hobson 2003]). In areas where Ovenbirds do breed in both edge and forest interior, edge-inhabiting birds often do poorly, suggesting that they are forced from preferred habitat and are making the best of a bad situation. However, they do not always have poor success in edge (Table 1). That Ovenbirds

may sometimes avoid forest interior and use only edge for breeding has not been previously reported.

A species with a wide breeding distribution might show geographic differences in habitat preferences, because habitat selection and use by breeding birds is based upon a complex mix of ultimate and proximate forces (Lack 1971, Cody 1985, Hutto 1985, Jones 2001). The costs and benefits of using available habitats may be influenced by predation, nest site, or food (Hutto 1985). In addition, intraspecific competition may force birds into marginal habitat (Fretwell and Lucas 1970), obscuring relationships between habitat preference, quality, and use. One would expect habitat use to vary if costs and benefits change geographically, even if the cues individuals use in selecting habitat are simple (e.g., a single element, such as light intensity, out of the multitude of features found in complex natural habitats).

Cues to habitat selection must be simple if

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TABLE 1. Regional variation in reproductive and pairing success of Ovenbirds in edge habitats versus forest interior in North America.

Location	Reproductive success ^a	Pairing success ^a	Reference
Northern Missouri	Lower	Lower	Van Horn et al. 1995
Central Missouri	? ^b	No difference ^c	Porneluzi and Faaborg 1999
Southern Indiana	No difference	?	Ford et al. 2001
New Jersey	?	Lower	Wander 1985
Northern Wisconsin	No difference	No difference	Flaspohler et al. 2001
North-central Minnesota	Lower	?	Manolis et al. 2002
Alberta	No difference	No difference	Lambert and Hannon 2000
Southern Saskatchewan	?	Lower	Bayne and Hobson 2001
Southern Saskatchewan	?	No difference	Mazerolle and Hobson 2003
Northern New Hampshire	No difference	No difference	King et al. 1996
Southern Ontario	Lower	Lower	Burke and Nol 1998
Quebec/Ontario	?	No difference	Villard et al. 1993

^a Along forest edge (0–100 m) as compared with interior.

^b No data.

^c $P > 0.05$, or as stated by authors.

they are genetically grounded (Lack 1971, Partridge 1978). Laboratory studies of habitat-choice cues by naive birds have supported the ideas of both genetic basis and cue simplicity (Partridge 1974). Morton (1990) showed that nonbreeding female Hooded Warblers (*Wilsonia citrina*) chose habitats with oblique trunks and branches, whereas males chose habitats with vertical structures, irrespective of vegetation height. Breeding habitat consists of a mix of these oblique and vertical habitat features (James 1971). Greenberg (1992) showed that both Swamp (*Melospiza georgiana*) and Song sparrows (*M. melodia*) choose habitat differing in a single cue, the presence of water, and that this cue was innate. Innate cues are one element in predicting settlement patterns and these are probably due to selection over ultimate time scales. Proximate cues are more likely to involve individual assessment of costs. Predators, for example, can make otherwise suitable habitat unusable (Block and Brennan 1993). General habitat-selection cues may coexist with microhabitat cues, such as those important in avoiding nest predation (Martin 1998). These factors have not been well studied.

Here, I report a study of habitat use by Ovenbirds in northwestern Pennsylvania, where they use only edge habitat contiguous to mature, deciduous forest-interior habitat. I show that this aberrant selection of breeding habitat appears to be influenced by predators, notably the eastern chipmunk (*Tamias striatus*). I also

describe a playback experiment designed to attract Ovenbirds to settle in forest-interior habitat. My results, and those of others, show that habitat usage may vary across diverse geographic areas.

METHODS

Study area.—The study took place at the 150-ha Hemlock Hill Biological Research Area (HHBRA), Crawford County, in northwestern Pennsylvania (41° 46' N, 79° 56' W), which is characterized by mature beech (*Fagus* spp.), maple (*Acer* spp.), oak (*Quercus* spp.), hickory (*Carya* spp.), and hemlock (*Tsuga* spp.) forest (Fig. 1; see also Howlett and Stutchbury 1996). Elevations range from 305 to 396 m and the terrain is largely flat or gently sloping. HHBRA is situated in an area fragmented by agriculture. Total forest cover for the region (740 km²) was 39% (Fraser and Stutchbury 2004) and 63% within a radius of 2 km of HHBRA (Rush 2004). HHBRA is surrounded by roads, fallow and active agricultural fields, and second-growth forest from 20 to 45 years old. To facilitate the mapping of territories, the entire 150-ha research area was grid-marked at 50-m intervals with orange plastic stakes in the ground and yellow flagging on trees. Beginning in 1971, and annually thereafter, I censused the entire area for breeding Ovenbirds. Censuses were conducted from 1 May to 1 July by listening for singing males, often in conjunction with ongoing studies of other species (e.g., Stutchbury et al.

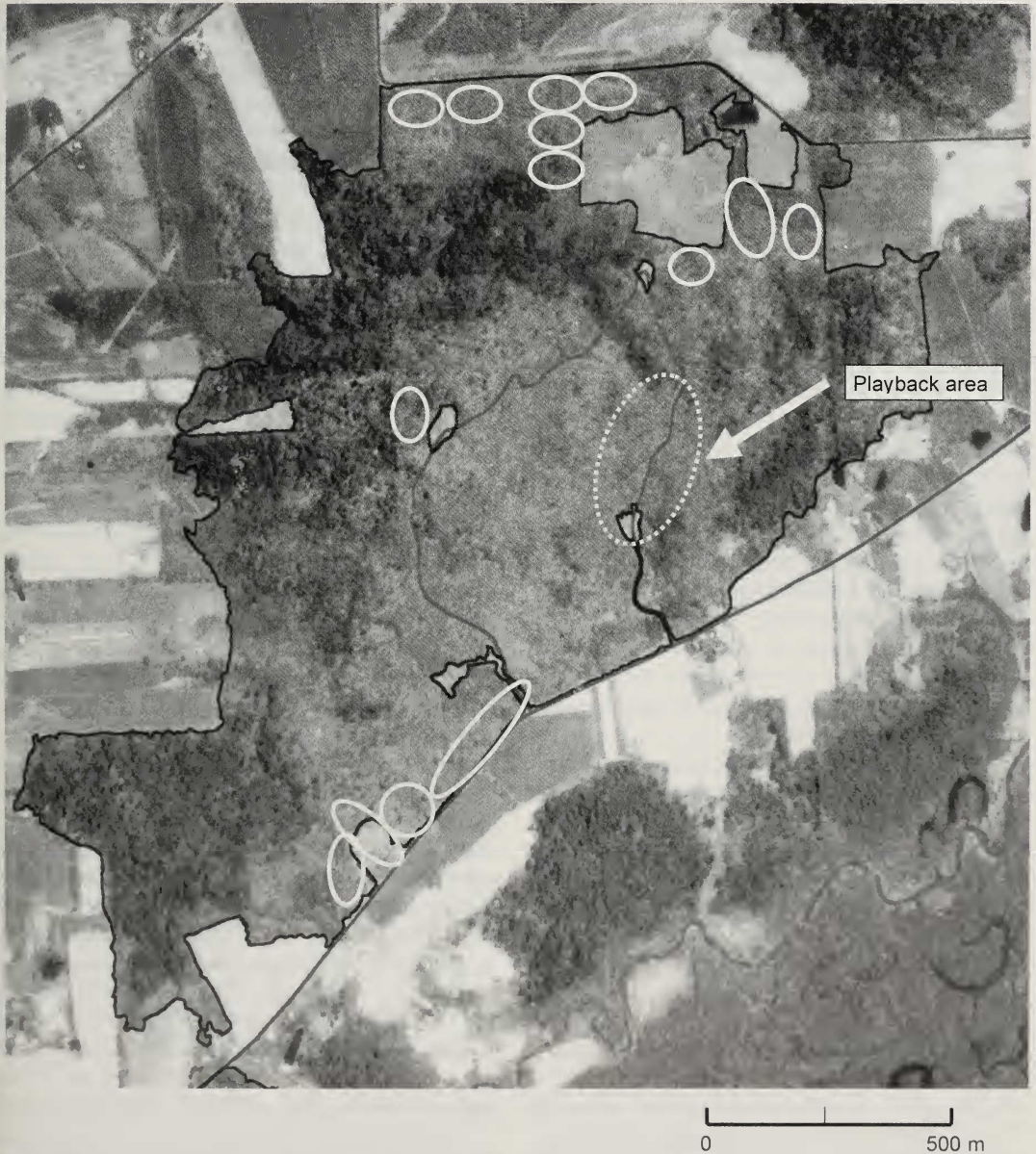


FIG. 1. Aerial photo of the Hemlock Hill Biological Research Area (HHBRA bordered in black) in northwestern Pennsylvania ($41^{\circ} 4' N$, $79^{\circ} 5' W$), taken in April 1994. Dark areas are dominated by eastern hemlock (*Tsuga canadensis*); deciduous forest is light-colored because trees were not yet leafed out. The entire Ovenbird population at the site ($n = 14$ pairs; territories depicted by white ovals) occurs in edge habitat. The 18-ha song playback area, indicated by the dashed oval, is in the interior of mature deciduous forest. A path can be seen going through the playback area and continuing in a loop through the forest. The four Ovenbird territories at the southern boundary abut a paved road bordering HHBRA; there are hay fields to the south of the road. No Ovenbirds have bred within the playback area over the past 33 years (1971 through 2003).

1994, Morton et al. 1998). Each year, 9–14 Ovenbird territories were detected at the same sites and only at forest edges (Fig. 1). To show differences in forest maturity, I established transects (50 m long) between two grid points to count and measure tree species and trunk diameters in Ovenbird territories ($n = 10$) and in areas not used by Ovenbirds ($n = 7$). All trees >5 cm diameter at breast height (dbh) and within 2 m of the transect line were tallied.

Hypotheses.—The 33 years of censuses at HHBRA showed that Ovenbirds bred in edge habitat in preference to forest interior. During this time, not a single breeding territory was located within the forest interior. With this background, in 2001–2003, I studied use of edge habitat by Ovenbirds at HHBRA in more detail, with the goal of testing why they might avoid forest-interior habitat. I tested several hypotheses: (1) Ovenbirds at HHBRA are nonbreeding, non-pairing transients; (2) food abundance is greater in edge habitat than in forest interior; and (3) Ovenbirds avoid using habitat with dense populations of eastern chipmunk, a potential predator.

I tested the first hypothesis by color banding all breeding males and mapping their territories each year. The pairing status of all males in the study area was assessed 5–10 times each year between late May and late June for the presence of mates. Returns by birds in subsequent years and acquiring mates and nesting would indicate that the Ovenbirds are not nonbreeding, non-pairing transients, but are breeders.

To test hypothesis 2, in 2003 I sampled litter depth on territories and compared those samples with random samples from the forest interior (unused habitat) following the protocol of Burke and Nol (1998). Those authors found that litter depth is positively correlated with food abundance for Ovenbirds, a ground-foraging species. I sampled litter depth at 10-m intervals along nine 50-m transects between grid points, six of which encompassed Ovenbird territories and three of which—randomly chosen—crossed forest-interior areas without breeding Ovenbirds.

Chipmunks are common forest and edge inhabitants in the research area and are predators on eggs, nestlings, and fledglings (Hill and Gates 1988, Reitsma et al. 1990, Fenske-

Crawford and Niemi 1997, King et al. 1998, Maier and DeGraaf 2000, Zegers et al. 2000). To test hypothesis 3, whether Ovenbirds avoid areas with many chipmunks, I assessed chipmunk prevalence by walking to a randomly chosen grid point, either within or outside of an Ovenbird territory. Once positioned there, I sat quietly on a folding chair and after 2 min began recording the time it took to detect (hear or see) a chipmunk within a radius of 25 m during the next 10 min. If no chipmunk was detected, a time of 600 sec was recorded. All chipmunk surveys were conducted on sunny, warm days from 09:30 to 11:30 EDT in July of 2001 and 2003. On- and off-territory chipmunk detection trials were paired for date, weather, and time of day. All on-territory trials were conducted in forest-edge habitat because there were no Ovenbird territories in the forest interior. Off-territory trials were either in forest interior within 200 m of an Ovenbird territory, or in an edge area unoccupied by Ovenbirds.

Playback study.—I conducted daily dawn-to-dusk playbacks of Ovenbird songs to induce settlement by simulating territorial occupation (Reed et al. 1999). A series of high-quality songs were recorded at normal singing cadence from one male breeding on the study site in 1985. Songs were played back continuously, except during heavy rains, from three Johnny Stewart Mini Wildlife Callers on 6-min TDK endless loop cassettes. Callers were located 100 m apart in the interior of mature deciduous forest. The broadcast covered an area of 18 ha (Fig. 1), determined by mapping points at distances from the speakers where the playback could just be detected by a human observer. The speaker locations were chosen because the mature forest surrounding them had no breeding Ovenbirds during the past 3 decades, and a trail allowed access. Speakers were placed 100 m apart, rather than randomly throughout the study area, because Ovenbird territories are clumped and a single, isolated speaker would not depict this normal situation. I conducted playback trials over two seasons. The first (16 July to 31 August 2001), consisted of 201 hr, 45 min of playback averaging 7 hr, 45 min per day and was designed to attract birds that were prospecting for territories for the next breeding season, spring 2002. The second series (24 April to 20 May

2003) ended when all traditional territories were filled and males were paired and nesting. This series consisted of 183 hr, 43 min of playback averaging 7 hr, 43 min per day, beginning at 06:00. Here, I wanted to see whether spring migrants could be attracted to settle immediately for the 2003 breeding season. Two-hr surveys for Ovenbirds that may have settled in response to playbacks were conducted every other day during the territory acquisition period (5 May to mid-June) in 2002 and 2003.

RESULTS

Ovenbird reproductive and pairing success varies among regions and studies. Edge habitat may be used, but with less reproductive success than in forest interior; it may be avoided; or, there may be little difference in nesting and pairing success (Table 1). Only at HHBRA and surrounding areas have Ovenbirds entirely avoided nesting in forest interior. I will first describe the situation at HHBRA and then report on the hypotheses testing mentioned above.

For 33 years, no Ovenbird territories occurred in the interior of the mature deciduous forest (Fig. 1). Instead, territories bordered roads, fields, and on one occasion in 2001, a large clearing for a gas well adjacent to a new clear-cut in the forest. Occupied areas were former agricultural fields abandoned in the 1950s and regrown with aspens (*Populus grandidentata* and *P. tremuloides*), American elms (*Ulmus americana*), and red maples (*Acer rubrum*).

On the ten 50-m transects through Ovenbird territories, there was a mean of 4.4 tree species and 15.2 ± 5.9 SD individual trees that averaged 13.7 ± 1.0 cm in dbh. The seven transects in interior forest had a mean of 6.3 tree species and 15.5 ± 2.5 individual trees that averaged 18.9 ± 12.8 cm in dbh. American beech (*Fagus americana*), hop hornbeam (*Ostrya carpinifolia*), American hornbeam (*Carpinus caroliniana*), and northern red oak (*Quercus borealis*) were found only in the forest-interior transects.

Transient versus breeding adults.—Annual return rates for banded males ($n = 14$ territories) were 67% in 2002 and 62% in 2003, within the normal range of return rates for male Ovenbirds; 85% were after-second-year

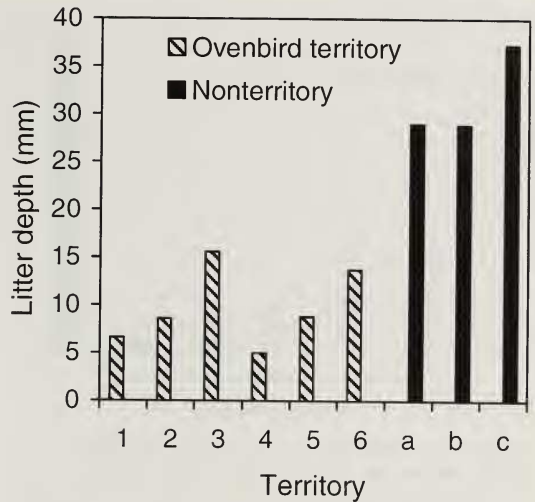


FIG. 2. Mean litter depth along 50-m transects (sampled every 10 m) in six different Ovenbird territories (1–6) and along three randomly placed forest-interior transects (a–c), northwestern Pennsylvania, 2003.

(ASY) birds. During the 2001–2003 study period, most males (86%) were paired—also within the normal range for forest-interior nesting birds in other studies (reviewed in Sabine et al. 1996, Burke and Nol 2001). I did not obtain information on breeding success, but young fledged successfully from four of four nests that were found incidentally. It is clear that these edge-inhabiting Ovenbirds were not transients, but were breeding adults that also had high pairing success and return rates.

Food abundance in edge habitat versus forest interior.—Mean litter depth was lower in Ovenbird territories ($1.64 \text{ cm} \pm 1.34$) than it was in forest-interior habitat ($3.17 \text{ cm} \pm 1.12$; Mann-Whitney test, $z = -4.95$, $P < 0.001$; Fig. 2). At HHBRA, litter depth in Ovenbird territories was less than that found on any territories in Ontario (Burke and Nol 1998); the same methods were used in both studies. In my forest-interior sample, litter depth (3.17 cm) was approximately the same as that found in Burke and Nol's (1998) most preferred nesting sites in large forest tracts. Insofar as litter depth is associated with food richness and nest-site preference in Ovenbirds (Burke and Nol 1998), we can reject the hypothesis that edge habitat at HHBRA offers more food

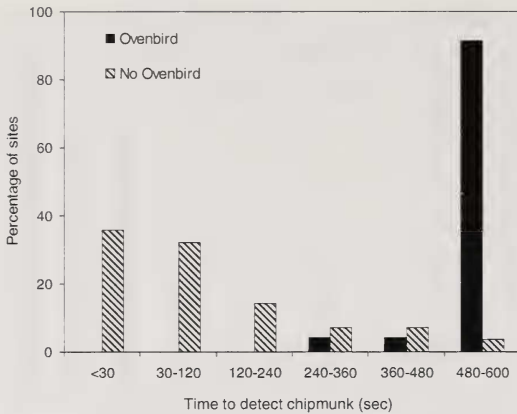


FIG. 3. Time (sec) to detect a chipmunk in the forest interior, unoccupied by Ovenbirds (hatched bars, $n = 28$), compared with the time to detect a chipmunk within Ovenbird territories (black bars, $n = 20$), north-western Pennsylvania, July 2001 and 2003. The maximum time allowed per point for chipmunk detection was 10 min. Chipmunks were rarely detected on Ovenbird territories but were abundant in forest interior.

and is more attractive to Ovenbirds than interior forest.

Chipmunk populations on and off Ovenbird territories.—Chipmunk presence was much greater off Ovenbird territories for each of the 2 years and for both years combined (Mann-Whitney test, $z = 4.87$, $P < 0.001$; Fig. 3). The average time to detect a chipmunk was only 2.1 min outside of Ovenbird territories, and chipmunks were found on 97% of the off-territory surveys. On Ovenbird territories, chipmunks were detected during only 3 of 21 surveys (14%) and it took an average of 7.2 min to detect them. Low chipmunk presence was not characteristic of all edge habitats at HHBRA and most edge did not hold Ovenbird territories (Fig. 1). In edge habitat not occupied by Ovenbirds ($n = 5$ surveys, randomly selected), it took an average of 66 sec to detect Chipmunks, similar to detection times in the forest-interior habitat unused by Ovenbirds. On one territory, occupied during 2001 and 2002, no chipmunks were observed in the 10-min surveys on it. This territory was unoccupied in 2003, and a survey then resulted in chipmunks detected in 5 min, 48 sec.

Playback study to induce Ovenbird settlement in forest interior.—Neither the late-summer nor the spring playbacks induced Ovenbirds to establish territories in the 18-ha for-

est-interior area (Fig. 1). Individuals were occasionally observed in the playback area during the spring playback series, but none sang or remained. Instead, territories were re-occupied in the traditional edge areas.

DISCUSSION

If one studied Ovenbirds only in north-western Pennsylvania, their habitat and behavior would be described as “forest edge; avoids mature interior forest!” This point highlights the need for assessing habitat use in many areas throughout a species’ range. For 33 years, Ovenbirds at HHBRA and the surrounding area have not settled in the interior of mature deciduous forest, despite low Ovenbird density and an abundance of what is usually considered “preferred” interior habitat. Although atypical, it may indicate that Ovenbirds are using nonhabitat cues when making decisions about whether or not to settle. An attempt to use playbacks to stimulate Ovenbird settlement in their preferred habitat at HHBRA failed. Summer playbacks failed to attract prospecting birds to settle the next breeding season and spring playbacks failed to induce settlement as well—although lone individuals were seen near the active playback speakers on several occasions.

The hypothesis that chipmunks—predators upon eggs, nestlings, and fledglings—deterred Ovenbirds from settling was supported. Chipmunks were nearly absent from Ovenbird territories during the 3-year study, but were abundant in the forest interior. It is possible that the Ovenbird territories at HHBRA are in edge habitats because some edge areas have low chipmunk numbers. If this is true, then the reasons for low chipmunk numbers should be perennial in the occupied edges; this appears to be the case. Chipmunks require an extensive burrow system for food storage, winter survival, and reproduction, but all Ovenbird-occupied edges were damp due to the presence of springs and poor drainage conditions; they also contained no large trees, whose root systems provide burrow support (Elliott 1978). In contrast, edges that supported chipmunk populations were drier and had large trees along former fence lines. Chipmunks are always common or abundant in our area (I have not recorded any year in which they were uncommon), perhaps due to the

abundance of both sugar (*Acer saccharum*) and red maples, trees that produce plentiful seed crops each year in fall and spring, respectively.

Could chipmunks be involved in habitat choice by Ovenbirds? As ground nesters and foragers, Ovenbirds are both particularly vulnerable to discovery by chipmunks and able to assess chipmunk density by directly encountering them during foraging or nest-site searching. The fact that Ovenbirds have an unusually short nestling period (8 days; Hann 1937) suggests that this species is under intense predation pressure (Bosque and Bosque 1995). Ovenbirds probably use litter depth (Burke and Nol 1998), as influenced by edaphic conditions (Smith 1977, Gibbs and Faaborg 1990, Blake et al. 1994), as a cue. Perhaps these direct habitat cues can be overshadowed by an assessment of chipmunk density. If so, then Ovenbirds at HHBRA might eschew forest interior there, where chipmunks are perennially common to abundant (ESM pers. obs.). As well, Ovenbird avoidance of chipmunks might have influenced the failure of playbacks to stimulate Ovenbirds to settle in the mature forest playback site (assuming they would respond to playbacks in the absence of chipmunks).

Some other ground-nesting species vulnerable to chipmunk predation also appear to choose nest sites that are chipmunk-free. For example, Dark-eyed Juncos (*Junco hyemalis*) and Louisiana Waterthrushes (*Seiurus motacilla*) place their nests only in recesses of vertical root balls of fallen trees (ESM pers. obs.). On the other hand, some forest ground nesters, such as Canada Warbler (*Wilsonia canadensis*), Black-and-white Warbler (*Mniotilta varia*), and Hermit Thrush (*Catharus guttatus*), do not exhibit this possible chipmunk avoidance ploy in their nest placement and are potential, but absent, breeders at HHBRA (ESM pers. obs.). Forstmeier and Weiss (2004) showed that Dusky Warblers (*Phylloscopus fuscatus*) exhibited adaptive plasticity in their nest-site selection. This tundra-inhabiting species places nests in safer and higher positions, at the expense of better microclimate and access to food, when Siberian chipmunk (*Tamias sibiricus*) populations are high. Forstmeier and Weiss (2004) suggested that Dusky Warblers, although short lived, are ca-

pable of assessing chipmunk numbers and selecting nests sites accordingly.

The evidence presented here on the importance of chipmunk activity precluding Ovenbirds from settling suggests the need for further experimental work. Future experiments could entail (1) removing chipmunks and then trying to attract Ovenbirds using playbacks, or (2) enticing chipmunks to invade traditional Ovenbird territories through food provisioning—and testing the prediction that Ovenbirds would no longer settle there. By altering chipmunk presence/absence, any definitive response in Ovenbird settlement would provide additional evidence that chipmunks afford cues to Ovenbirds when choosing nesting habitats.

The importance of looking for general, simple cues to habitat selection is clear. However, nearly all studies of habitat-selection cues have been of temperate zone birds whose territoriality coincides with reproduction. Avenues of habitat selection in tropical birds with yearlong territories, where biotic interactions are features of habitat requirements, await discovery. Mixed-species flocks or ant/acacia mutualisms are examples (Janzen 1969, Terborgh 1985, Marra and Remsen 1997, Stutchbury and Morton 2001). Habitat studies of birds should proceed beyond general descriptions, such as “forest interior” or “area sensitive,” for these terms may constrain, rather than enhance, explanations of habitat use (Villard 1998).

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